AD 411876

UNIVERSITY OF MARYLAND

THE INSTITUTE FOR FLUID DYNAMICS

and

APPLIED MATHEMATICS

4 NA   5 440 500

14 Technical Note BN/322   11 June 1963, 12 32p. 13 NA

6 A MATHEMATICAL ANALYSIS OF THE STEPPING
STONE MODEL OF GENETIC CORRELATION,* 7 - 7 NA

10 by

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* This research was supported in part by the Office of Naval [redacted]der grant Nonr 595(17).

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ABSTRACT

In this paper we analyze the correlation coefficient between members of any two colonies out of an infinite ensemble of colonies. It is assumed that each colony has the same number of members, that migration takes place between the different colonies , and that there is a constant rate of mutation in each colony. An explicit formula is derived for the correlation function and the long distance form of this function is derived. It is shown that under rather weak restrictions on the pattern of migration the asymptotic form of the correlation function is characteristic of the dimension of the model.

1. Introduction

The theory of evolution postulates the development of a species by the fixation of mutant genes. Since the doctrine of survival of the fittest is no longer recognized to hold in its strictest form one can understand differences in a given species in terms of the development and viability of several alternate genes for the same characteristic. Clearly, geographic separation between two colonies of the same species would tend to promote genetic differences between members of the two colonies. One can interpret the formation of separate races in this light. It is the purpose of this paper to analyze a mathematical model which supplies quantitative information on the effects of distance and dimensionality on genetic differences between groups isolated by distance. The model was first proposed by one of us (M. K.), [1], and a discussion of the biological implications of this work will appear in Genetics, [2]. The present paper is devoted strictly to the mathematical development.

Wright was the first one to discuss quantitatively the phenomenen of isolation by distance. He considered a large population in which there are several groups, and analyzed the inbreeding coefficient of a subgroup relative to the large population by means of his method of path coefficients, [3-5]. Malécot has calculated correlation coefficients for a continuous model roughly similar to ours, [6,7].

The present model considers an infinite number of colonies, each colony containing N individuals. It will be assumed that breeding proceeds by generations, and that migration may take place between colonies in a manner to be specified more precisely below. We will also allow mutations to take place at a finite rate. In this way the composition of each colony will change randomly due to these three causes. We shall calculate the correlation coefficients $E(p(i)\ p(i+j))$ where $p(i)$ is the frequency of one of the alleles in colony i. We ignore effects due to the finiteness of the number of colonies, and we shall only be interested in the equilibrium state of the system, i. e., the question of the time of spread of a gene through a population will not be treated here.

We shall begin by deriving the difference equations which describe the stepping stone model in any number of dimensions. Then we shall specialize to the one, two, and three dimensional cases when migration is allowed between adjacent colonies only. Finally, we shall discuss the modifications which must be made when longer range migration is allowed. It will be shown that under certain conditions restricting the magnitude of long range migration the form of the correlation function at long distances is that predicted by allowing the difference equations to be approximated by a differential equation. The present work, in its mathematical details, is the discrete version of the theory of multidimensional random processes recently discussed by Whittle, [8].

2. Formulation of the Model

Let us consider an array of colonies; for simplicity we can think of them as being found on the coordinate points of a cartesian grid which will be extended to infinity in all directions. The coordinates of a point will be denoted by $\underset{\sim}{k} = (k_1, k_2, \dots, k_n)$ where only the cases n = 1, 2, or 3 are of any interest, these corresponding to a linear habitat, a two dimensional dwelling area, and a three dimensional dwelling area. The latter is proposed as a model for microorganisms in the ocean. By convention we assume that the components, k_j, range over all integers, positive and negative.

The gene frequency of allele A_1 at site $\underset{\sim}{k}$ will be denoted by $p(\underset{\sim}{k})$. In our model the gene frequency at any site changes in any generation by three mechanisms. These are:

1. Exchange between the given subgroup and any other subgroup.
2. Mutation, or equivalently, exchange between the given subgroup and one located at infinity.
3. Random sampling of gametes in the process of reproduction.

It will be assumed that migration and reproduction occur periodically, allowing us to deal with epochs rather than with a continuous time variable.

For simplicity we shall set up the equations for the $E(p(i)\,p(i+j))$ in the one dimensional case. Then we shall indicate the extension to the n dimensional case. In one dimension we let m_j denote the probability of exchange between the colony at $k = 0$ and the colonies

at $+j$ and $-j$. Since we shall only deal with a symmetric situation the probability of exchange between $k=0$ and $k=j$ will be $m_j/2$. If $p(k)$ denotes the gene fraction of A_1 at k at a given epoch and $p'(k)$ denotes the gene fraction of A_1 at k at the next epoch, we can write

$$p'(k) = \left(1 - \sum_{j=1}^{\infty} m_j - m_\infty\right) p(k) + \frac{m_1}{2}\left(p(k+1) + p(k-1)\right) + \frac{m_2}{2}\left(p(k+2) + p(k-2)\right) + \cdots + m_\infty \bar{p} + \xi(k) \tag{2.1}$$

where $\xi(k)$ is a random variable which represents the change due to random sampling of gametes, and $\bar{p}$ is the expected fraction of gene A_1 in any of the colonies. The term $m_\infty \bar{p}$ represents the effects of mutation in changing $p(k)$. If it is assumed that there is no selection of gene A_1 then $\xi(k)$ has the properties with respect to expectation:

$$E(\xi(k)) = 0, \qquad E(\xi^2(k)) = \frac{p(k)\,(1 - p(k))}{2N_e} \tag{2.2}$$

where N_e is the effective (constant) size of each subgroup. This parameter is defined in terms of N_m the number of males and N_f, the number of females by

$$\frac{1}{N_e} = \frac{1}{4}\left(\frac{1}{N_m} + \frac{1}{N_f}\right). \tag{2.3}$$

Equation (2.1) can be cast into a simpler form by defining a new variable

$$\tilde{p}(k) = p(k) - \bar{p} \tag{2.4}$$

which eliminates the term $m_\infty \bar{p}$. Furthermore we will only be concerned with the equilibrium case so that we may put

$$\tilde{p}'(k) = \tilde{p}(k). \tag{2.5}$$

Finally, in order to rewrite Eq. (2.1) in a simpler form we shall introduce a shift operator S. This operator is defined by the properties:

$$S f(i) = f(i+1), \qquad S^{-1} f(i) = f(i-1) \tag{2.6}$$

Making the changes indicated, we can write the equilibrium equation for $\tilde{p}(k)$ as

$$\tilde{p}(k) = \Big[\Big(1 - \sum_{j=1}^{\infty} m_j - m_\infty\Big) + \frac{m_1}{2}(S + S^{-1}) + \frac{m_2}{2}(S^2 + S^{-2}) + \\ + \cdots \Big]\tilde{p}(k) + s(k) \tag{2.7}$$

or

$$\tilde{p}(k) = L\tilde{p}(k) + s(k) \tag{2.8}$$

where L is the operator

$$L = \Big(1 - \sum_{j=1}^{\infty} m_j - m_\infty\Big) + \sum_{j=1}^{\infty} \frac{m_j}{2}(S^j + S^{-j}). \tag{2.9}$$

In higher dimensions the operator L takes on a more complicated looking form because there are more indices. For example in two dimensions with a rectangular coordinate system it is necessary to introduce two shift operators S_1 and S_2 having the properties

$$\begin{aligned} S_1 f(i,j) &= f(i+1, j) \\ S_2 f(i,j) &= f(i, j+1) \end{aligned} \tag{2.10}$$

The general form of L is then

$$L = 1 - \sum_{i,j=0}^{\infty} m_{ij} - m_{00} + \sum_{i,j=0}' \frac{m_{ij}}{4} (s_1^{i} + s_1^{-i})(s_2^{j} + s_2^{-j}) \tag{2.11}$$

where the prime denotes omission of the term $i = j = 0$.

In this paper, our principal concern will be the calculation of the correlation function which we denote by $r(\underline{k})$ and which will be defined by the relation

$$r(\underline{k}) = \frac{E[\tilde{\varphi}(\underline{k})\,\tilde{\varphi}(\underline{0})]}{E[\tilde{\varphi}^2(\underline{0})]} = \frac{\rho(\underline{k})}{\rho(\underline{0})} \tag{2.12}$$

where $\rho(\underline{k})$ is the unnormalized correlation function.

In order not to be burdened by an excess of notation let us return to the one dimensional case to derive the equation satisfied by $r(k)$

If we multiply Eq.(2.1) by $\tilde{\varphi}(0)$ and take expectations we find for $k \neq 0$ the result

$$\rho(k) = E[L\,\tilde{\varphi}(k)\,L\,\tilde{\varphi}(0)] \tag{2.13}$$

However, it is shown in Appendix A that

$$E[L\tilde{\varphi}(k)\,L\,\tilde{\varphi}(0)] = E[L^2\tilde{\varphi}(k)\,\tilde{\varphi}(0)] = L^2\rho(k). \tag{2.14}$$

Hence $r(k)$ satisfies the equation

$$(1 - L^2)\, r(k) = 0, \qquad k \neq 0. \tag{2.15}$$

This result is also valid in higher dimensions since the argument which led to this equation does not refer to the number of dimensions. In the case of $\rho(0)$ we must take into account the expression for the variance

given in Eq. (2.2). The value of $\rho(0)$ is therefore to be found from

$$(1-L^2)\rho(0) = \frac{\bar{p}-\overline{p^2}}{2N_e} = \frac{\bar{p}(1-\bar{p})-\rho(0)}{2N_e}. \tag{2.16}$$

3. <u>Exact Solution to the Equations</u>

We now turn to a discussion of the solution to Eqs. (2.14) and (2.16). A necessary and sufficient condition that a set of numbers $\{r_n\}$ to be a correlation function is that it admits of a spectral representation, [9]. Hence it is natural to assume a solution of the form

$$r(k) = \frac{1}{(2\pi)^n}\int_0^{2\pi}\!\!\cdots\!\int F(\theta_1, \theta_2, \ldots \theta_n)\cos k_1\theta_1 \ldots \cos k_n\theta_n \, d\theta_1 \ldots d\theta_n \tag{3.1}$$

and try to determine the function $F(\theta_1, \theta_2, .. \theta_n)$. We will carry out the detailed calculation for $n=1$ and indicate the generalization to higher dimensions. Substituting Eq. (3.1) with $n=1$ into Eq. (2.15) we find that

$$\int_0^{2\pi} F(\theta)\,(1-L^2)\cos k\theta \, d\theta = 0, \qquad k \neq 0. \tag{3.2}$$

It will now be demonstrated that

$$(1-L^2)\cos k\theta = (1-H^2(\cos\theta))\cos k\theta \tag{3.3}$$

where $H(\cos\theta)$ is an ordinary function of $\cos\theta$. For simplicity let us set $m_0 = 1 - \sum_{j=1}^{\infty} m_j - m_\infty$. Then

$$\begin{aligned} L^2\cos k\theta &= \sum_{j=0}^{\infty}\frac{m_j}{2}(S^j + S^{-j})\sum_{i=0}^{\infty}\frac{m_i}{2}(S^i + S^{-i})\cos k\theta \\ &= \frac{1}{4}\sum_{i=0}^{\infty}\sum_{j=0}^{\infty} m_i m_j (S^{i+j} + S^{i-j} + S^{-i+j} + S^{-i-j})\cos k\theta \end{aligned} \tag{3.4}$$

by straightforward multiplication. But the result of operating on $\cos k\theta$ by the operator in parentheses is

$$(S^{i+j} + S^{i-j} + S^{-i+j} + S^{-i-j}) \cos k\theta \tag{3.5}$$

$$= \cos(k+i+j)\theta + \cos(k+i-j)\theta + \cos(k-i+j)\theta + \cos(k-i-j)\theta$$

$$= 2\cos k\theta\,[\cos(i+j)\theta + \cos(i-j)\theta]$$

$$= 4\cos k\theta \cos i\theta \cos j\theta$$

Thus we find for $L^2 \cos k\theta$ the expression

$$L^2 \cos k\theta = \sum_{i=0}^{\infty}\sum_{j=0}^{\infty} (m_i m_j \cos i\theta \cos j\theta) \cos k\theta \tag{3.6}$$

$$= \Big(\sum_{j=0}^{\infty} m_j \cos j\theta\Big)^2 \cos k\theta = H^2(\cos\theta)\cos k\theta$$

where $H(\cos\theta) = \sum_{j=0}^{\infty} m_j \cos j\theta$.

Replacing the operator L by $H^2(\cos\theta)$ in Eq. (3.2) we find

$$\int_0^{2\pi} F(\theta)(1 - H^2(\cos\theta)) \cos k\theta \, d\theta = 0, \quad k \neq 0. \tag{3.7}$$

This is clearly satisfied if we choose $F(\theta)$ to be

$$F(\theta) = \frac{1}{1 - H^2(\cos\theta)}. \tag{3.8}$$

The general solution for $r(k)$ can therefore be given in the form

$$r(k) = \frac{C}{2\pi}\int_0^{2\pi} \frac{\cos k\theta \, d\theta}{1 - H^2(\cos\theta)}, \quad k \neq 0. \tag{3.9}$$

The constant C can be fixed by the requirement that $r(0) = 1$. This procedure yields the result valid for all k;

$$r(k) = \frac{\frac{1}{2\pi}\int_0^{2\pi} \frac{\cos k\theta \, d\theta}{1 - H^2(\cos\theta)}}{\frac{1}{2\pi}\int_0^{2\pi} \frac{d\theta}{1 - H^2(\cos\theta)}} = \frac{\frac{1}{4\pi}\int_0^{2\pi} \cos k\theta \left[\frac{1}{1 - H(\cos\theta)} + \frac{1}{1 + H(\cos\theta)}\right] d\theta}{\frac{1}{4\pi}\int_0^{2\pi} \left[\frac{1}{1 - H(\cos\theta)} + \frac{1}{1 + H(\cos\theta)}\right] d\theta} \tag{3.10}$$

In higher dimensions the same reasoning leads to the representation:

$$r(\underline{k}) = \frac{\dfrac{1}{(2\pi)^n} \int_0^{2\pi} \cdots \int \dfrac{\cos k_1\theta_1 \cos k_2\theta_2 \cdots \cos k_n\theta_n \, d\theta_1 \, d\theta_2 \cdots d\theta_n}{1 - H^2(\cos\theta_1, \cos\theta_2, \ldots, \cos\theta_n)}}{\dfrac{1}{(2\pi)^n} \int_0^{2\pi} \cdots \int \dfrac{d\theta_1 \, d\theta_2 \cdots d\theta_n}{1 - H^2(\cos\theta_1, \cos\theta_2, \ldots, \cos\theta_n)}} \tag{3.11}$$

Finally, we return to the calculation of $\rho(0)$ from Eq. (2.16) now knowing the values of the $r(k)$. The general procedure for finding this quantity is to substitute $\rho(0)\, r(k)$ for the value of $\rho(k)$. In this way we find

$$\rho(0)\left[(1-L^2)\, r(0)\right] = \frac{\bar{p}(1-\bar{p})}{2N_e} - \frac{\rho(0)}{2N_e} \tag{3.12}$$

which is also true in higher dimensions.

The value of $(1-L^2)r(0)$ is found from the representation of Eq. (3.11) using the identity of (3.6). We have, in fact

$$(1-L^2)\, r(0) = \frac{1}{\dfrac{1}{2\pi}\displaystyle\int_0^{2\pi} \dfrac{d\theta}{1-H^2(\cos\theta)}} \tag{3.13}$$

which implies the expression for $\rho(0)$:

$$\rho(0) = \frac{\bar{p}(1-\bar{p})}{1+2N_e(1-L^2)r(0)} = \frac{\bar{p}(1-\bar{p})}{1+\dfrac{4N_e\pi}{\displaystyle\int_0^{2\pi}\dfrac{d\theta}{1-H^2(\cos\theta)}}} \tag{3.14}$$

When $m_1 = m_2 = \cdots = 0$ but m_∞ is greater than zero then

$$\rho(0) = \frac{\bar{p}(1-\bar{p})}{1 + 2N_e m_\infty (2 - m_\infty)} \tag{3.15}$$

which agrees with a result given earlier by Wright, [3]. The result analogous to Eq. (3.10) holds also in higher dimensions.

4. Specific Solutions to the General Equations

In this section we shall present a study of several specific examples using the general techniques so far developed. In addition we shall derive an asymptotic expression for $r(k)$ under the assumption that $k^2 = k_1^2 + k_2^2 + \cdots + k_n^2$ is large. The simplest example is that of a linear habitat in which migration can accur between adjacent colonies only. For this case only m_1 differs from zero and the function $H(\cos\theta)$ is given by

$$H(\cos\theta) = 1 - m_\infty - m_1(1 - \cos\theta). \tag{4.1}$$

The relevant integrals can all be derived from the single formula

$$\frac{1}{2\pi}\int_0^{2\pi} \frac{\cos n\theta \, d\theta}{x + \cos\theta} = \frac{1}{\sqrt{x^2-1}}\left(\sqrt{x^2-1} - x\right)^n, \quad x > 1 \tag{4.2}$$

$$= \frac{(-1)^{n+1}}{\sqrt{x^2-1}}\left(x + \sqrt{x^2-1}\right)^n, \quad x < -1.$$

With these results we find for $r(k)$

$$r(k) = \frac{A_1(k) + A_2(k)}{A_1(0) + A_2(0)} \tag{4.3}$$

where

$$A_1(k) = \frac{1}{2\sqrt{2m_1 m_\infty + m_\infty^2}} \left[1 + \frac{m_\infty}{m_1} - \sqrt{2\left(\frac{m_\infty}{m_1}\right) + \left(\frac{m_\infty}{m_1}\right)^2} \right]^k \qquad (4.4)$$

$$A_2(k) = \frac{1}{2\sqrt{(2-m_1-m_\infty)^2 - m_1^2}} \left[\sqrt{\left(\frac{2-m_\infty-m_1}{m_1}\right)^2 - 1} - \frac{2-m_\infty-m_1}{m_1} \right]^k .$$

Although the solutions so far have been perfectly general, there are approximations possible in writing the solution based on the fact that

$$m_\infty \ll m_j \qquad (4.5)$$

for all realistic situations. In fact we shall generally assume that m_1 is of the order of 10^{-1} and m_∞ is roughly 4×10^{-5}. This implies that $A_2(k)$ is small in comparison to $A_1(k)$. This is also true in higher dimensions. For example, in the present case, with the parameters that we have just mentioned

$$\begin{aligned} A_1(k) &= 177\ (.972)^k \\ A_2(k) &= 0.263\ (-0.26)^k . \end{aligned} \qquad (4.6)$$

It will be noted that with the present, general method of solution, one does not have to choose the solutions with the property $r(k) \to 0$ This condition is insured by the trigonometric representation of $r(k)$ given in Eq. (3.11) and the Riemann-Lebesgue lemma, [10].

Let us next consider a two dimensional rectangular lattice of colonies in which migration can take place only to the nearest neighboring colonies, as pictured in Fig. 1. To be completely general let us suppose that migration in the x direction is different from that in the y direction. We may use the general form of Eq. (3.11) and introduce the function of two variables $H(\cos\theta_1, \cos\theta_2)$ by

$$H(\cos\theta_1, \cos\theta_2) = 1 - m_\infty - m_1(1-\cos\theta_1) - m_2(1-\cos\theta_2). \quad (4.7)$$

The two integrals which figure in the evaluation of $r(n_1, n_2)$ are:

$$A_1(n_1,n_2) = \frac{1}{8\pi^2}\int_0^{2\pi}\int_0^{2\pi}\frac{\cos n_1\theta_1 \cos n_2\theta_2 \, d\theta_1 \, d\theta_2}{m_\infty + m_1(1-\cos\theta_1) + m_2(1-\cos\theta_2)} \quad (4.8)$$

$$A_2(n_1,n_2) = \frac{1}{8\pi^2}\int_0^{2\pi}\int_0^{2\pi}\frac{\cos n_1\theta_1 \cos n_2\theta_2 \, d\theta_1 \, d\theta_2}{2 - m_\infty - m_1(1-\cos\theta_1) - m_2(1-\cos\theta_2)}.$$

These may be transformed into single integrals which preserve the symmetry inherent in them by use of the identity

$$\frac{1}{a} = \int_0^\infty e^{-at}\,dt \quad (4.9)$$

to put the denominators in an exponential form. In this way we find that $A_1(n_1,n_2)$ and $A_2(n_1,n_2)$ can be expressed alternatively as

$$A_1(n_1,n_2) = \frac{1}{8\pi^2}\int_0^\infty e^{-(m_\infty + m_1 + m_2)t} \, dt \quad . \quad (4.10)$$

$$\cdot \int_0^{2\pi}\int_0^{2\pi}\cos n_1\theta_1 \cos n_2\theta_2 \, e^{m_1 t\cos\theta_1} e^{m_2 t \cos\theta_2} \, d\theta_1 \, d\theta_2$$

$$A_2(n_1, n_2) = \frac{1}{8\pi^2} \int_0^\infty e^{-(2-m_\infty-m_1-m_2)t}\, dt \int_0^{2\pi}\!\!\int_0^{2\pi} \cos n_1\theta_1 \cos n_2\theta_2 \cdot$$

$$\cdot\, e^{-m_1 t \cos\theta_1}\, e^{-m_2 t \cos\theta_2}\, d\theta_1\, d\theta_2 .$$

The step of interchanging orders of integration can be justified in detail. The angular integrations can be carried out by means of the Bessel function representation, [11],

$$\frac{1}{2\pi} \int_0^{2\pi} \cos n\theta\, e^{mt\cos\theta}\, d\theta = I_n(mt) \qquad (4.11)$$

where $I_n(x)$ is a Bessel function of imaginary argument. In this way we find

$$A_1(n_1, n_2) = \frac{1}{2} \int_0^\infty e^{-(m_\infty+m_1+m_2)t}\, I_{n_1}(m_1 t)\, I_{n_2}(m_2 t)\, dt \qquad (4.12)$$

$$A_2(n_1, n_2) = \frac{(-1)^{n_1+n_2}}{2} \int_0^\infty e^{-(2-m_\infty-m_1-m_2)t}\, I_{n_1}(m_1 t)\, I_{n_2}(m_2 t)\, dt .$$

It is clear from this representation that for the values of m_∞, m_1 and m_2 considered here $A_1(n_1, n_2)$ is always greater than the absolute value of $A_2(n_1, n_2)$ since $I_n(x)$ is positive for $x > 0$ and the quantity $m_\infty + m_1 + m_2$ is much less than $2 - m_\infty - m_1 - m_2$.

The diagonal terms $A_{1,2}(n,n)$ can be evaluated exactly in terms of Legendre functions of the second kind or in terms of complete elliptic integrals. It is known that

$$\int_0^\infty e^{-at} J_n(bt) J_n(ct)\,dt = \frac{1}{\pi\sqrt{bc}}\, Q_{n-\frac{1}{2}}\left(\frac{a^2+b^2+c^2}{2bc}\right) \tag{4.13}$$

so that if we replace b by ib and c by ic we obtain

$$\int_0^\infty e^{-at} I_n(bt) I_n(ct)\,dt = \frac{(-1)^n}{\pi i\sqrt{bc}}\, Q_{n-\frac{1}{2}}\left(\frac{b^2+c^2-a^2}{2bc}\right) \tag{4.14}$$

where the argument of the Legendre function is negative since $a > b+c$. For $n=0$ we use the integral respresentation of the Legendre function to transform this into a form more convenient for calculation:

$$Q_{-\frac{1}{2}}(-z) = \frac{1}{\sqrt{2}}\int_0^\pi \frac{dt}{\sqrt{-z-\cos t}} = i\sqrt{2}\int_0^{\pi/2}\frac{d\theta}{\sqrt{z+1-2\sin^2\theta}} \tag{4.15}$$

$$= i\sqrt{\frac{2}{1+z}}\; K\left(\frac{2}{1+z}\right)$$

where

$$K(k^2) = \int_0^{\pi/2}\frac{d\theta}{\sqrt{1-k^2\sin^2\theta}} \tag{4.16}$$

is a complete elliptic integral of the first kind. Thus the normalizing constant C is found from

$$C^{-1} = \frac{1}{\pi}\left[\frac{1}{\sqrt{m_\infty^2+2m_\infty(m_1+m_2)+4m_1m_2}}\, K\left(\frac{1}{1+\frac{m_\infty}{2}\left(\frac{1}{m_1}+\frac{1}{m_2}\right)+\frac{m_\infty^2}{4m_1m_2}}\right) \right. \tag{4.17}$$

$$\left. + \frac{1}{\sqrt{(2-m_\infty-m_1)(2-m_\infty-m_2)}}\, K\left(\frac{2}{2+\frac{(2-m_\infty)^2}{2m_1m_2}-(2-m_\infty)\left(\frac{1}{m_1}+\frac{1}{m_2}\right)}\right)\right]$$

When m_∞ / m_1 and m_∞ / m_2 are small in comparison to 1 we may derive a simpler expression for C^{-1}. Let us consider the first elliptic integral in Eq. (4.17) and set

$$\epsilon = \frac{m_\infty}{2}\left(\frac{1}{m_1} + \frac{1}{m_2}\right) + \frac{m_\infty^2}{4 m_1 m_2} \tag{4.18}$$

i. e., ϵ is also small in comparison to 1. The argument $(1+\epsilon)^{-1}$ is therefore close to 1 and we may then approximate the elliptic integral by

$$K\left(\frac{1}{1+\epsilon}\right) = \ln \frac{4}{\sqrt{\epsilon}} + O(\epsilon \ln \epsilon). \tag{4.19}$$

In the second elliptic integral to appear in Eq. (4.17) we notice that the term

$$\frac{(2-m_\infty)^2}{2 m_1 m_2} - (2-m_\infty)\left(\frac{1}{m_1} + \frac{1}{m_2}\right) \tag{4.20}$$

is large in comparison with 1 so that the argument is small. We can therefore use the approximation

$$K(\eta) = \frac{\pi}{2}\left[1 + \frac{\eta}{4} + \frac{9}{64}\eta^2 + O(\eta^3)\right]. \tag{4.21}$$

Hence an approximate value for C^{-1} is

$$C^{-1} = \frac{1}{\pi}\,\frac{1}{\sqrt{4 m_1 m_2 + 2 m_\infty (m_1 + m_2)}}\,\ln \frac{4}{\sqrt{\frac{m_\infty}{2}\left(\frac{1}{m_1} + \frac{1}{m_2}\right)}} \tag{4.22}$$

$$+ \frac{1}{2}\,\frac{1}{\sqrt{(2-m_\infty)^2 - 2(2-m_\infty)(m_1 + m_2)}}\left[1 + \frac{1}{2\left(2 + \frac{(2-m_\infty)^2}{2 m_1 m_2} - (2-m_\infty)\left(\frac{1}{m_1} + \frac{1}{m_2}\right)\right)}\right]$$

We have neglected terms of the order of m_∞^2/m_1^2 and m_∞^2/m_2^2 since these are $O(10^{-6})$ for all problems of interest.

Exact results can be obtained for the diagonal elements by recursion. The expression for $\rho(n,n)$ is

$$\rho(n,n) = \frac{1}{2\pi\sqrt{m_1 m_2}}\Big[Q_{n-\frac{1}{2}}\Big(-1 - m_\infty\Big(\frac{1}{m_1}+\frac{1}{m_2}\Big) - \frac{m_\infty^2}{2m_1m_2}\Big) \tag{4.23}$$

$$+ Q_{n-\frac{1}{2}}\Big(-1 - \frac{(2-m_\infty)^2}{2m_1m_2} + (2-m_\infty)\Big(\frac{1}{m_1}+\frac{1}{m_2}\Big)\Big)\Big].$$

We have already related $Q_{-\frac{1}{2}}(-z)$ to the complete elliptic integral $K\left(\frac{2}{1+z}\right)$. A similar calculation shows that

$$Q_{\frac{1}{2}}(z) = i\sqrt{2(z+1)}\,E\Big(\frac{2}{z+1}\Big) - iz\sqrt{\frac{2}{z+1}}\,K\Big(\frac{2}{z+1}\Big) \tag{4.24}$$

where $E(x)$ is the complete elliptic integral of the second kind

$$E(k^2) = \int_0^{\pi/2}\sqrt{1-k^2\sin^2\theta}\,d\theta. \tag{4.25}$$

Values of $Q_{n-\frac{1}{2}}(-z)$ for $n > 1$ can be obtained from the recurrence relation, [11]

$$Q_{n+\frac{1}{2}}(-z) = \frac{2z}{2n+1}\Big[(n-\tfrac{1}{2})Q_{n-3/2}(-z) - 2n\,Q_{n-\frac{1}{2}}(-z)\Big]. \tag{4.26}$$

It does not seem possible to derive values of $\rho(n_1,n_2)$ in general for $m_1 \neq m_2$ in terms of tabulated functions. However, in the symmetric case, $m_1 = m_2$, it is possible to derive expressions for $\rho(n_1,n_2)$ either by appealing to the difference equation or by returning to the integral expression for the A's. For example to get $\rho(0,1)$ we

note that when $m_1 = m_2$

$$A(0,1) = A(1,0) = \frac{1}{2}\left[A(0,1) + A(1,0)\right]. \tag{4.27}$$

Hence

$$A_1(0,1) + A_2(0,1) = \frac{1}{2}\left(2 + \frac{m_0}{m_1}\right) A_1(0,0) + \frac{1}{2}\left(2 - \frac{2-m_0}{m_1}\right) A_2(0,0) \tag{4.28}$$

from which $\rho(0,1)$ can be calculated. In theory it would be possible to build up a complete set of the $\rho(n_1, n_2)$ for the symmetric case by recurrence. However, this quickly becomes tedious and is indeed quite special because of the restriction $m_1 = m_2$. Hence we turn to a different range, namely large values of $n_1 + n_2$.

For large $n_1 + n_2$ another approach is possible. Let us return to the expression of $A_{1,2}(n_1, n_2)$ in terms of trigonometric integrals (Eq. (4.8)). We can write the expression for $A_1(n_1, n_2)$ as

$$A_1(n_1, n_2) = \frac{1}{2\pi^2} \int_0^{\pi}\int_0^{\pi} \frac{\cos n_1\theta_1 \cos n_2\theta_2 \, d\theta_1 \, d\theta_2}{m_0 + m_1(1-\cos\theta_1) + m_2(1-\cos\theta_2)} \tag{4.29}$$

by symmetry.

A similar reduction in the area of integration of $A_2(n_1, n_2)$ also holds. In the limit $n_1, n_2 \to \infty$ we notice by asymptotic arguments similar to those given by Duffin, [12], that the main contribution to the integral comes from the neighborhood of $(\theta_1, \theta_2) \sim (0,0)$ since the denominator is a minimum there. Hence the integral can be approximated by expanding the denominator around $(0,0)$:

$$A_1(n_1,n_2) \sim \frac{1}{2\pi^2}\int_0^{\pi}\int_0^{\pi} \frac{\cos n_1\theta_1 \cos n_2\theta_2 \, d\theta_1 d\theta_2}{m_0 + \frac{m_1}{2}\theta_1^2 + \frac{m_2}{2}\theta_2^2}\,. \tag{4.30}$$

Again, in the limit $n_1, n_2 \to \infty$ the limits of integration can be fixed as $(0,\infty)$ with an exponentially small error. Thus we find

$$A_1(n_1,n_2) \sim \frac{1}{2\pi^2}\int_0^{\infty}\int_0^{\infty} \frac{\cos n_1\theta_1 \cos n_2\theta_2 \, d\theta_1 d\theta_2}{m_0 + \frac{m_1\theta_1^2}{2} + \frac{m_2}{2}\theta_2^2} \tag{4.31}$$

$$= \frac{1}{\pi^2\sqrt{m_1 m_2}}\int_0^{\infty}\int_0^{\infty} \frac{\cos\left(n_1\sqrt{\frac{1}{m_1}}\,x_1\right)\cos\left(n_2\sqrt{\frac{1}{m_2}}\,x_2\right) dx_1 dx_2}{2m_0 + x_1^2 + x_2^2}\,.$$

In a similar way it can be shown that an approximate expression for $A_2(n_1,n_2)$ is

$$A_2(n_1,n_2) \sim \frac{(-1)^{n_1+n_2}}{\pi^2\sqrt{m_1 m_2}}\int_0^{\infty}\int_0^{\infty} \frac{\cos\left(n_1\sqrt{\frac{1}{m_1}}\,x_1\right)\cos\left(n_2\sqrt{\frac{1}{m_2}}\,x_2\right) dx_1 dx_2}{2(2-m_0-2(m_1+m_2)) + x_1^2 + x_2^2}\,. \tag{4.32}$$

Both of these integral depend, aside from the trigonometric factors, only on $x_1^2 + x_2^2$. Bochner has shown, [13], that if an integral is of the form

$$U(\alpha_1,\alpha_2,\dots\alpha_n) = \int_{-\infty}^{\infty}\cdots\int f(x_1,x_2,\dots x_n)\,e^{-i(\alpha_1 x_1+\dots+\alpha_n x_n)}\,dx_1 dx_2\dots dx_n \tag{4.33}$$

where $f(x_1, x_2, \ldots, x_n) = \varphi(\sqrt{x_1^2 + x_2^2 + \cdots + x_n^2})$ then $U(\alpha_1, \alpha_2, \ldots \alpha_n)$ depends only on the quantity $\alpha = (\alpha_1^2 + \alpha_2^2 + \cdots + \alpha_n^2)^{1/2}$ and the integral can be reexpressed as

$$U(\alpha) = \frac{(2\pi)^{n/2}}{\alpha^{\frac{n-2}{2}}} \int_0^\infty \varphi(\rho)\rho^{n/2} J_{\frac{n-2}{2}}(\alpha\rho)\, d\rho \tag{4.34}$$

where $J_{\frac{n-2}{2}}(t)$ is the Bessel function of order $\frac{n}{2} - 1$.

In the present case we may set

$$\alpha = \left(\frac{n_1^2}{m_1} + \frac{n_2^2}{m_2}\right)^{1/2} \tag{4.35}$$

and

$$A_1(n_1, n_2) \sim \frac{1}{4\pi\sqrt{m_1 m_2}} \int_0^\infty \frac{\rho J_0(\alpha\rho)\, d\rho}{2m_\infty + \rho^2} = \frac{1}{4\pi\sqrt{m_1 m_2}} K_0(\sqrt{2m_\infty}\,\alpha) \tag{4.36}$$

by [11] where $K_0(u)$ is a modified Bessel function of the third kind. In a similar way we find that $A_2(n_1, n_2)$ is

$$A_2(n_1, n_2) \sim \frac{(-1)^{n_1 + n_2}}{4\pi\sqrt{m_1 m_2}} K_0\left(\alpha\sqrt{2(2 - m_\infty - 2m_1 - 2m_2)}\right). \tag{4.37}$$

The parameters m_1 and m_2 are of the order of magnitude of 5×10^{-2} and m_∞ is roughly 4×10^{-5}. Hence if n_1 and n_2 are both 5 or greater then α is greater than 70 and the argument in the Bessel function approximation for $A_1(n_1, n_2)$ is roughly 6 while the argument in the expression for $A_2(n_1, n_2)$ is over 100.

Considering that the function $K_0(x)$ has the asymptotic expansion

$$K_0(x) \sim \sqrt{\frac{\pi}{2x}}\, e^{-x} \tag{4.38}$$

we see that $A_2(n_1, n_2)$ is negligible in comparison with $A_1(n_1, n_2)$ and that for $n_1, n_2 \geq 5$ one can satisfactorily write for

$$r(n_1,n_2) = \frac{1}{2C}\sqrt{\frac{1}{2\pi m_1 m_2}}\left(2\,\frac{m_\infty n_1^2}{m_1} + 2\,\frac{m_\infty n_2^2}{m_2}\right)^{-1/4} \times \tag{4.39}$$

$$\times \exp\left\{-\left(\frac{2m_\infty}{m_1}n_1^2 + \frac{2m_\infty}{m_2}n_2^2\right)^{1/2}\right\} .$$

In particular if $m_1 = m_2$ and we set $\sqrt{n_1^2 + n_2^2} = R$, we find

$$r(R) = \frac{1}{2\sqrt{2\pi}}\,\frac{1}{m_1 C}\left(\frac{m_1}{2m_\infty}\right)^{1/4}\frac{e^{-R\sqrt{\frac{2m_\infty}{m_1}}}}{\sqrt{R}} . \tag{4.40}$$

Thus we see that in contrast to the one dimensional case in which the correlation falls off exponentially at large distances, the two dimensional correlation function falls off as an exponential divided by $\sqrt{R}$.

It might be objected that such a conclusion depends critically on our model, i. e., that if longer range migrations are included the asymptotic form of the correlation function would be changed. In the next section we shall show that if the long range migrations are sufficiently weak the general form of the correlation function will remain unchanged except that m_1 and m_2 are replaced by different combinations of the m's.

A closer analysis shows that the next term in the expansion is of the order of

$$\frac{e^{-R\sqrt{\frac{2m_\infty}{m_1}}}}{R}$$

which is smaller than the result of Eq. (4.40) by a factor of $\sqrt{R}$

Finally we may turn to the three dimensional case in which migration is characterized by three exchange coefficients, m_1, m_2, and m_3 as shown in Fig. 2. For this case we use the same reasoning as in two dimensions and thereby find the results

$$A_1(n_1,n_2,n_3) = \frac{1}{2\pi^3}\iiint_0^\pi \frac{\cos n_1\theta_1 \cos n_2\theta_2 \cos n_3\theta_3 \, d\theta_1 d\theta_2 d\theta_3}{m_\infty + m_1(1-\cos\theta_1) + m_2(1-\cos\theta_2) + m_3(1-\cos\theta_3)} \tag{4.41}$$

$$= \frac{1}{2}\int_0^\infty e^{-(m_\infty+m_1+m_2+m_3)t} I_{n_1}(m_1 t) I_{n_2}(m_2 t) I_{n_3}(m_3 t)\, dt$$

(4.41)

$$A_2(n_1,n_2,n_3) = \frac{1}{2\pi^3}\iiint_0^\pi \frac{\cos n_1\theta_1 \cos n_2\theta_2 \cos n_3\theta_3 \, d\theta_1 d\theta_2 d\theta_3}{2 - m_\infty - m_1(1-\cos\theta_1) - m_2(1-\cos\theta_2) - m_3(1-\cos\theta_3)}$$

$$= \frac{(-1)^{n_1+n_2+n_3}}{2}\int_0^\infty e^{-(2-m_\infty-m_1-m_2-m_3)t} I_{n_1}(m_1 t) I_{n_2}(m_2 t) I_{n_3}(m_3 t)\, dt .$$

In this case, an expression in closed form for $\rho(0,0,0)$ is known only for $m_\infty = 0$ and $m_1 = m_2 = m_3$, otherwise numerical methods must be used. Fortunately tables are available which are useful for the case $m_1 = m_2$ [14]. This is the case of isotropic migration in a plane but a different amount of migration in the third dimension. Such a model would be useful to describe the composition of an oceanic habitat in which it might be supposed that there is no distinction between the two directions of horizontal migration, but there is a distinction between migration in a horizontal or a vertical direction. The tables in [14] are expressed in terms of the function

$$I(a,b,c;\alpha;\beta) = \frac{1}{\pi^3}\int\int\int_0^{\pi} \frac{\cos ax \cos by \cos cz \; dx\,dy\,dz}{(2+\alpha)\beta - \cos x - \cos y - \alpha\cos z}. \tag{4.42}$$

Performing the necessary reductions, we can express the A's in terms of this triple integral:

$$A_1(n_1,n_2,n_3) = \frac{1}{2m_1} I\left(n_1,n_2,n_3;\ \frac{m_3}{m_1};\ 1 + \frac{m_\infty}{2m_1+m_3}\right) \tag{4.43}$$

$$A_2(n_1,n_2,n_3) = \frac{(-1)^{n_1+n_2+n_3}}{2m_1} I\left(n_1,n_2,n_3;\ \frac{m_3}{m_1};\ \frac{2-m_\infty}{2m_1+m_3} - 1\right).$$

The value of $\rho(0,0,0)$ must be obtained from the tables. When $n_1^2 + n_2^2 + \frac{m_1}{m_3} n_3^2$ is much greater than 1, the value of $\rho(n_1,n_2,n_3)$ is given by the asymptotic expansion:

$$\rho(n_1, n_2, n_3) = \sqrt{\frac{m_1}{m_3}}\ \frac{1}{4\pi R}\ e^{-AR} \tag{4.44}$$

where

$$R^2 = n_1^2 + n_2^2 + \frac{m_1}{m_3} n_3^2 \tag{4.45}$$
$$A^2 = 2\left(2 + \frac{m_3}{m_1}\right)\left(\frac{m_\infty}{2m_1 + m_3}\right) .$$

In particular if $m_1 = m_3$ then the correlation function has the characteristic form

$$\rho(n_1, n_2, n_3) = \frac{e^{-R\sqrt{\frac{3m_\infty}{m_1}}}}{4\pi R} \tag{4.46}$$

where $R^2 = n_1^2 + n_2^2 + n_3^2$. This is seen to fall off much more quickly than the one or two dimensional cases. Corrections to Eq. (4.46) are given in [14].

In Figure 3 we have plotted, for the purpose of comparison some results for one, two, and three dimensions. In these we have set $m_\infty = 4 \times 10^{-5}$ and all of the other m's are set equal to one another. In one dimension we have put $m_1 = 0.1$, in two dimensions $m_1 = m_2 = 0.05$ and in three dimensions $m_1 = m_2 = m_3 = 0.0333$. It can be seen that an increase in the number of dimensions has a critical effect on $r(\underline{n})$.

5. General Interactions

So far we have restricted ourselves to a rectangular lattice with migration permitted between nearest colonies only. It might be thought that the conclusions that we have drawn concerning the long range form of the correlation function depend on the particular model we have chosen, and that if longer range migrations are allowed our conclusions are incorrect. We shall show that if the long-range migration is sufficiently weak, in a sense to be specified more exactly, the correlation function retains the same form for long distances as that found for near colony migration. For simplicity we shall derive the result in one dimension and indicate the extension to higher dimensional habitats. The reasoning for these remains exactly the same.

In one dimension the representation of Eq. (3.10) is valid. For large n we expand $A_1(n)$ and $A_2(n)$ as indicated in Eq. (4.30). For $A_1(n)$ we find

$$A_1(n) = \frac{1}{2\pi}\int_0^{\pi} \frac{\cos n\theta \, d\theta}{m_\infty + m_1(1-\cos\theta_1) + m_2(1-\cos 2\theta) + \cdots} \qquad (5.1)$$

$$\sim \frac{1}{2\pi}\int_0^{\infty} \frac{\cos n\theta \, d\theta}{m_\infty + \frac{\theta^2}{2}\sum_{j=1}^{\infty} j^2 m_j}$$

$$= \frac{1}{2\sqrt{2m_\infty \mu_2}}\, e^{-n\sqrt{\frac{2m_\infty}{\mu_2}}}$$

where we have defined the parameter μ_2 by

$$\mu_2 = \sum_{j=1}^{\infty} j^2 m_j \, . \tag{5.2}$$

Thus it can be seen that under the hypothesis that μ_2 is finite $A_1(n)$ decreases exponentially with n, the coefficient of n being $-(2m_\infty/\mu_2)^{1/2}$ as was found earlier for the special case of nearest colony migration. The function $A_2(n)$ for large n is given, in the same manner, by

$$A_2(n) \sim \frac{(-1)^n}{\sqrt{2\mu_2(2-m_\infty-2\mu_0)}} \, e^{-n\sqrt{\frac{2(2-m_\infty-2\mu_0)}{\mu_2}}} \tag{5.3}$$

in which

$$\mu_0 = \sum_{j=1}^{\infty} m_j \tag{5.4}$$

It is necessary to find the value of $\rho(0)$ by some numerical or approximate method in the present instance. Notice that the inequality

$$1 \geq m_\infty + \mu_0 \tag{5.5}$$

always implies that $A_1(n) \geq |A_2(n)|$, or that the first term is always dominant in the limit $n \to \infty$. However, the possibility of long range migration can make the contribution of $A_2(n)$ significant in the range of n which may be of interest.

In two dimensions we must consider an array of quantities $\{m_{ij}\}$ in which m_{ij} is the percentage of the colony at $(0, 0)$ which is exchanged with the colony at (i, j). In terms of these quantities, and auxiliary functions μ_{rs} defined by

$$\mu_{rs} = \sum_{j=0}^{\infty} \sum_{i=0}^{\infty} i^r j^s m_{ij} \tag{5.6}$$

we find in two dimensions that

$$A_1(n_1, n_2) \sim \frac{1}{\pi\sqrt{\mu_{02}\mu_{20}}} K_0\left(\alpha\sqrt{2m_{00}}\right) \tag{5.7}$$

$$A_2(n_1, n_2) \sim \frac{(-1)^{n_1+n_2}}{\pi\sqrt{\mu_{02}\mu_{20}}} K_0\left(\alpha\sqrt{2(2-m_{00}-2\mu_{02}-2\mu_{20})}\right)$$

where

$$\alpha^2 = \frac{n_1^2}{\mu_{20}} + \frac{n_2^2}{\mu_{02}} . \tag{5.8}$$

Thus we see that the only difference between results derived for nearest colony migration and for the present unrestricted case is that m_1 and m_2 are to be replaced by μ_{10} and μ_{02} respectively. When μ_{20} and μ_{02} are not finite this account is not valid and other forms are possible for $r(n_1, n_2)$.

However when migration can take place between a finite group of colonies only, the asymptotic form of the correlation function will always be as given in Eq. (5.7). The conclusions for the three dimensional case case are also the same.

Results for different periodic arrangements of colonies resemble those given in this paper. Formal expressions can be derived for $r(\underline{k})$ in terms of multiple trigonometric integrals as in the present analysis. The conclusions which can be drawn concerning the long distance form of $r(\underline{k})$ are the same as given in the present paper, and depend most significantly on the dimensionality of the habitat. Naturally, the value of $r(\underline{k})$ for small k varies between different types of lattices and must be calculated individually. One can write down a continuous version of the present model. The analysis leads to partial differential equations analogous to our partial difference equations, and indeed the same form of $r(\underline{k})$ for large k can be recovered. However, in two and three dimensions the solutions to the partial differential equations are singular at the origin and ad hoc methods are required to fix the normalizing constant. It is therefore felt that the present model is a more accurate representation of reality.

Acknowledgement: We would like to acknowledge the gracious hospitality of Professor James F. Crow and the Department of Medical Genetics at the University of Wisconsin. We would also like to acknowledge several enlightening discussions with Professor Crow and Professor Sewall Wright.

Appendix A: Proof of the Equality $E\left[L\tilde{p}(k)\, L\tilde{p}(0)\right] = E\left[L^2\tilde{p}(k)\,\tilde{p}(0)\right]$

In this appendix we prove the equality stated in the title for the one dimensional case. A simple extension of the notation suffices to prove the result for higher dimensions. The proof is straightforward and consists of a direct calculation of the terms involved. We may write for the left side of the equation

$$E\left[L\tilde{p}(k)\, L\tilde{p}(0)\right] = \frac{1}{4} E\left[\sum_{j=0}^{\infty} m_j (S^j + S^{-j})\tilde{p}(k) \sum_{r=0}^{\infty} m_r (S^r + S^{-r})\tilde{p}(0)\right]$$

$$= \frac{1}{4} E\left[\sum_{j=0}^{\infty} m_j \left(\tilde{p}(k-j) + \tilde{p}(k+j)\right) \sum_{r=0}^{\infty} m_r \left(\tilde{p}(-r) + \tilde{p}(r)\right)\right]$$

$$= \frac{1}{4} E\Big[\sum_{j=0}^{\infty} \sum_{r=0}^{\infty} m_j m_r \big(\tilde{p}(r)\tilde{p}(k+j) + \tilde{p}(-r)\tilde{p}(k+j)$$

$$+ \tilde{p}(r)\tilde{p}(k-j) + \tilde{p}(-r)\tilde{p}(k-j)\Big]$$

$$= \frac{1}{4} \sum_{j=0}^{\infty} \sum_{r=0}^{\infty} m_j m_r \big(\rho(k+j-r) + \rho(k+j+r) + \rho(k-j-r)$$

$$+ \rho(k-j+r)\big).$$

For the right side we find

$$E\left[L^2\tilde{\rho}(k)\tilde{\rho}(0)\right] = E\left[\tilde{\rho}(0)\,L^2\tilde{\rho}(k)\right]$$

$$= \frac{1}{4}E\left[\tilde{\rho}(0)\sum_{j=0}^{\infty}\sum_{r=0}^{\infty} m_j m_r \left(S^j + S^{-j}\right)\left(S^r + S^{-r}\right)\tilde{\rho}(k)\right]$$

$$= \frac{1}{4}\sum_{j=0}^{\infty}\sum_{r=0}^{\infty} m_j m_r \left(\rho(k+j+r) + \rho(k+j-r) + \rho(k+r-j) + \rho(k-r-j)\right)$$

$$= E\left[L\tilde{\rho}(k)\,L\tilde{\rho}(0)\right].$$

Another proof of this equality can be derived by means of the soectral representation of $\tilde{\rho}(k)$. [9]

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Figure Captions:

Fig. 1. Plot of $r(k)$ as a function of k for one, two, and three dimensions.

Fig. 2. Schematic representation of exchange between colonies in a two dimensional habitat.

Fig. 3. Schematic representation of exchange between colonies in a three dimensional habitat.

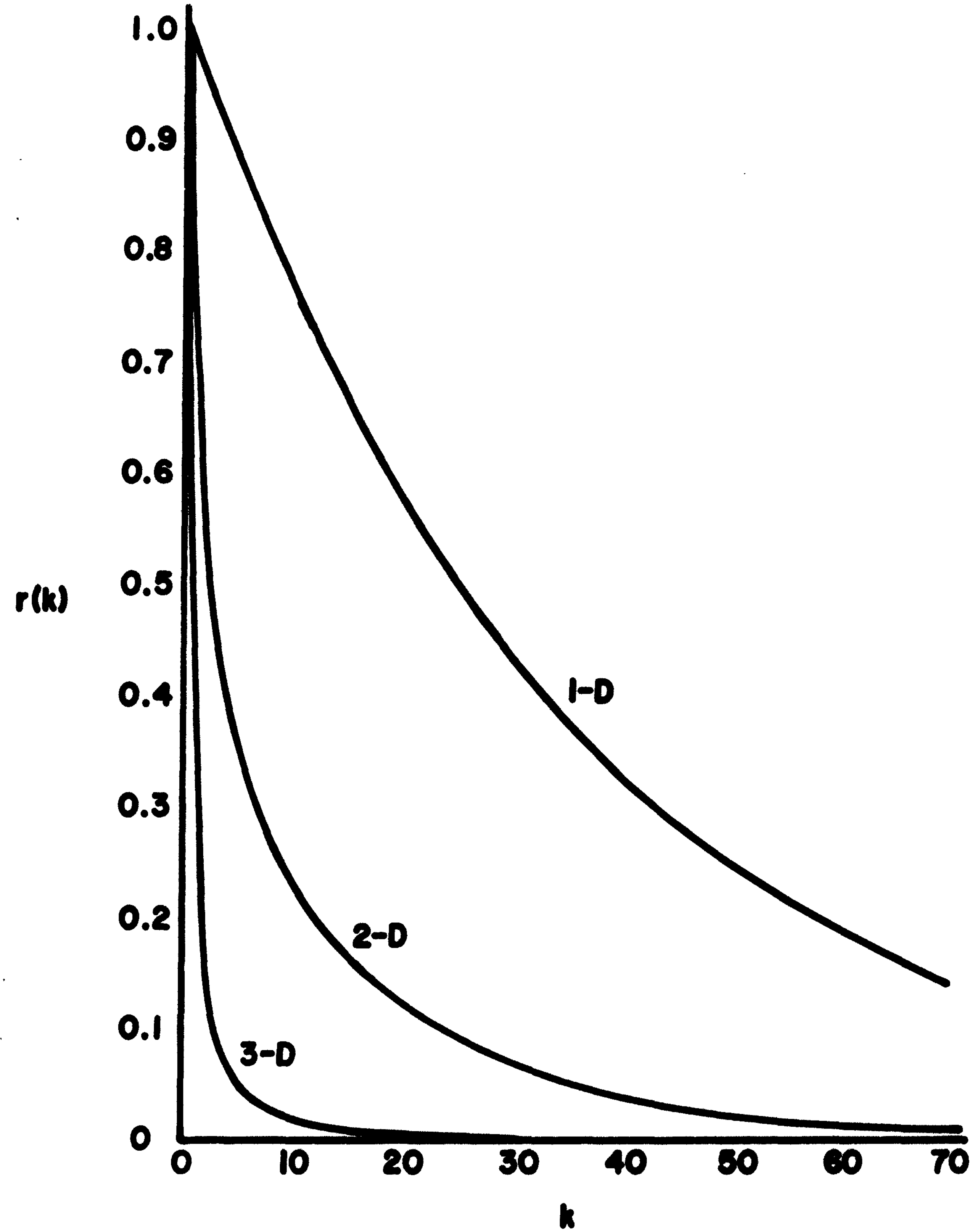

FIG. 1

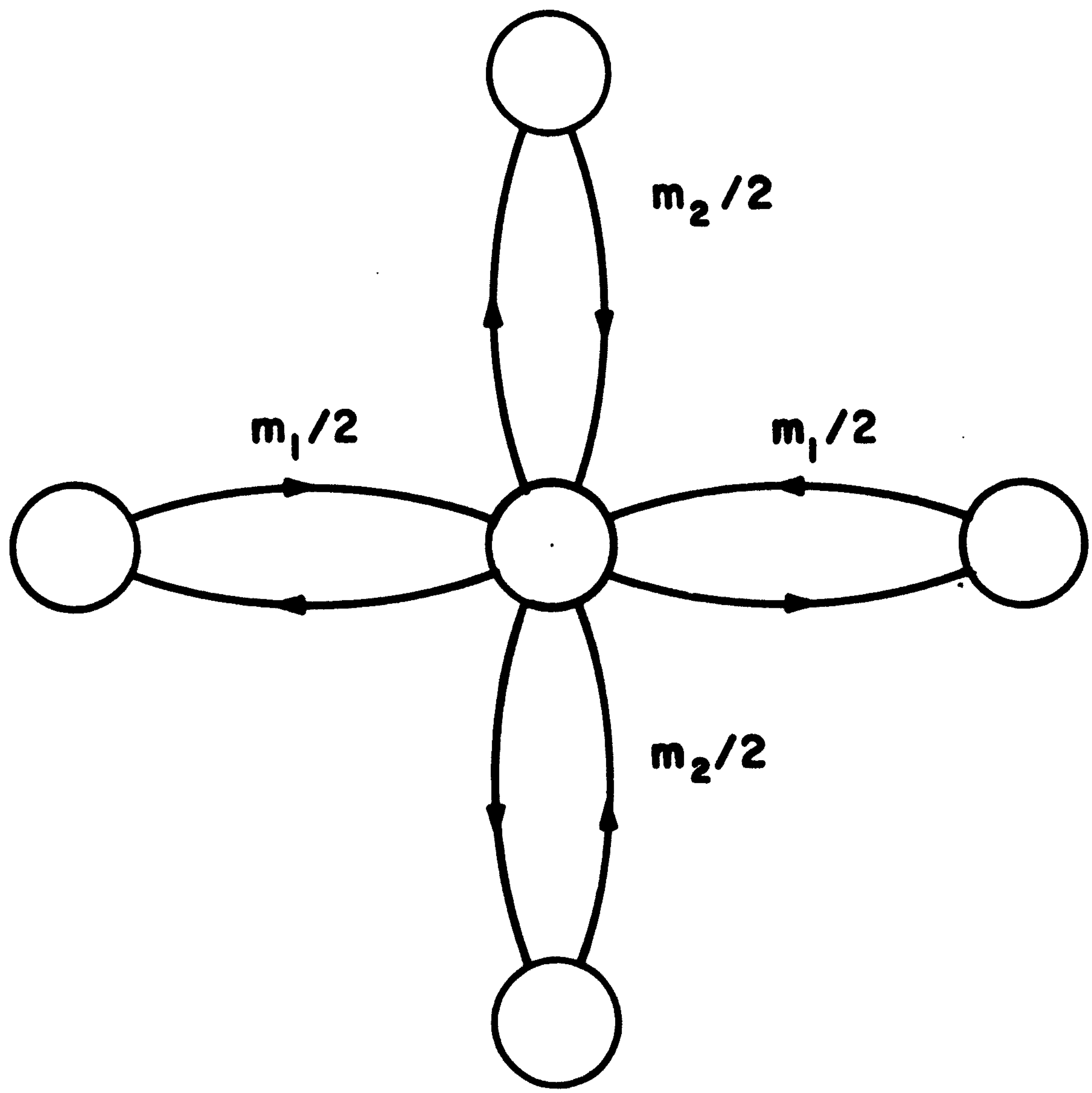

FIG. 2

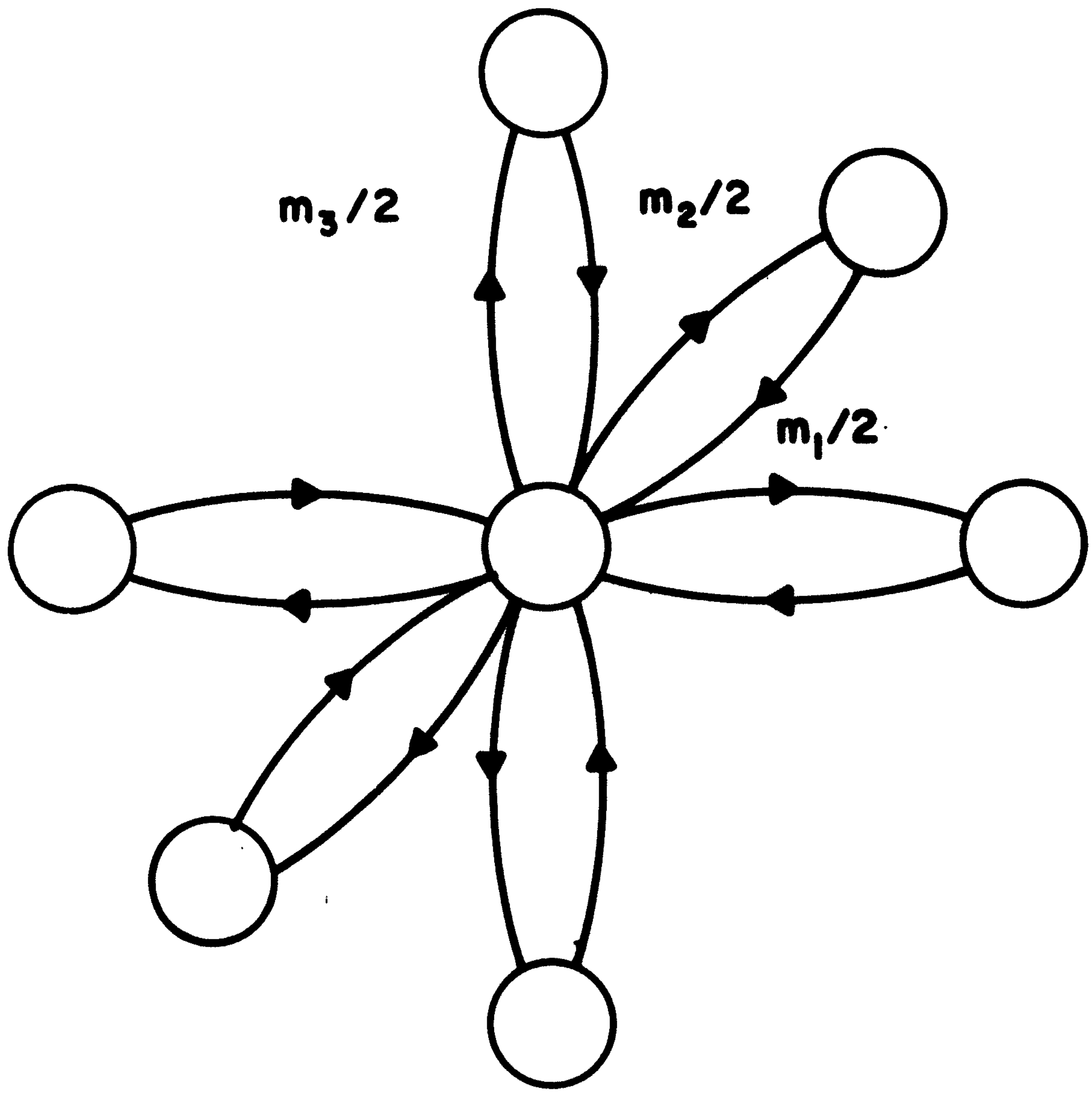

FIG. 3